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THE SIGNIFICANCE OF SCUTE AND PLATE "ABNORMALITIES" IN CHELONIA.

A CONTRIBUTION TO THE EVOLUTIONARY HISTORY OF THE CHELONIAN CARAPACE AND PLASTRON.

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IV. THE TAIL-TRUNK OF CHELYDRA SERPENTINA AS A CLOSE APPROXIMATION TO ANCESTRAL CONDITIONS OF CARAPACE AND PLASTRON.

Baur, Hay and others have used as the hypothetical ancestral form an aberrant and perhaps highly specialized Chelonian, *Dermachelys coriacea*, but in the light of the various atavistic recurrences discussed in this paper and in view of the fact that certain definite rows of scutes invariably predominate over others, I have been led to seek elsewhere for primitive conditions.

A closer approximation to the true ancestral conditions is, I believe, to be seen in that portion of the trunk of *Chelydra* that is commonly called the base of the tail. Here if anywhere one would expect to find primitive conditions. The Chelydridæ are generally acknowledged to be our most generalized chelonians, and it is natural to look for primitive characters in this family, especially in the less specialized regions of the body.

A careful study of the portion of the body posterior to the carapace, which for convenience may be called the "tail-trunk," is fruitful of suggestions. A preparation of the bony structures of this region was made from a very large specimen (Fig. 58) measuring nearly three feet from snout to tip of tail, having a carapace sixteen inches long and a tail-trunk fifteen inches long. The preparation shows the following structures:

There are 33 vertebræ ranging in size from very large bones of nearly a cubic inch displacement to very minute ossicles at the tip of the tail. The first five vertebræ are beneath the carapace and have their dorsal processes in close contact with a longitudinal bony ridge that traverses the last three plates of the neural row of the carapace. These five vertebræ have definite flattened ribs that project laterally about at right angles to the axis of the vertebral column and remind one of the flattened ribs in the carapace of *Dermochelys*. The first and second of these ribs are very large and articulate by means of enlarged heads with the proximal ends of the ileum. These specialized vertebræ and ribs form the sacrum (Fig. 58, 1 and 2).

Surmounting the dorsal processes of the eighth to the fifteenth vertebra is a row of six large bony tubercles (*t.* 1 to 6) that have no reference to individual vertebræ. The dorsal processes of the latter are not the centers of ossification for the tubercles and there is no articulation or fusion between the two series of structures. Posterior to the sixth bony tubercle are fourteen tubercles (*y.* 1–14), with either membraneous cores or no cores at all, ranging in size from structures almost as large as the sixth bony tubercle to extremely small scales with dorsal ridges. Anterior to the first bony tubercle are three small soft tubercles (*x*) occurring at intervals of about half an inch, and anterior to these we find the two procaudal (*pr.* 1 and 2) and the single pygal plate (*p*) of the carapace, overlying the first four vertebræ. We have then the following heterogeneous series of structures: two procaudals, one pygal, three small soft tubercles, six large tubercles with bony cores and finally a graduated series of 14 tubercles merging into ridged scales. It seems reasonable to suppose that all these structures of the dorsal row, whether scutes with bony cores, scutes without bony cores, or bony plates that have been separated from their original scute coverings, are essentially homogeneous, and that the differences seen in the different regions are secondary or perhaps tertiary modifications. It seems probable that the scutes at the posterior end of the row represent the most primitive condition, which, through a process of continuous variation have become more tubercular in form and have acquired bony cores by the gradual ossification of membraneous tissue. The three soft tubercles surmounting the fifth to seventh vertebræ probably represent a reduced condition in adaptation to the fact that the base of the tail requires flexibility and must be swung from side to side or partially withdrawn under the carapace. The presence of such large prominences as the bony tubercles would seriously interfere with the mobility of the tail. The procaudal plates seem to have been the last of the neural tubercles to have been flattened out to form the dermal carapace. The last neural scute is probably the original chitinous sheath of one of the procaudals, doubtless the second one. The scute of the first procaudal I believe to have been crowded out in the process of scute reduction that will be discussed later.

Over the 33 vertebræ there occur 27 structures of homogeneous origin, that may be designated scutes. This number is sufficiently at variance with the number of vertebræ to preclude the possibility that they have had a segmental arrangement. Moreover, their irregular arrangement and the dermal origin of the bony cores make it certain that they are independent structures, in opposition to views expressed by Gadow and others.

An examination of the entire tail-trunk of another large specimen revealed the rather striking fact that the number of principal rows of tubercles and large scutes in this region is identical with that of the carapace and plastron, and that smaller, less regular rows of tubercles and scales represent the principal lost rows. A section of the tail-trunk was slit down the median ventral line and flattened out for convenience in drawing, and from this the somewhat diagrammatic Fig. 55 was constructed. I was able with certainty to homologize seven principal rows, three dorsal, two lateral and two ventral, and have named them after their homologues in the carapace and plastron, neurals (*N*), costals (*C*), marginals (*M*), and plastrals (*P*). Smaller and less regular rows of tubercles and scales are homologized with the secondary and lost rows as follows : inframarginals (*IM*), supramarginals (*SM*), interplastrals (*IP*), and neuro-costals (*NC*), a row not occurring in any modern species. In the following more detailed description the above names will be used for the rows concerned.

The costals are large scutes with a marked tendency toward dorsi-ventral flattening. Their apices are directed posteriorly and the growing point is thus situated near the posterior margin of the scute, a fact that causes the scute to grow anteriorly and laterally and very little posteriorly. The marginals are as large as the costals and are flattened so as to expose two surfaces, a dorsal and a ventral. The apex is directed away from the axis of the body and the growth of the scute is principally inward and slightly forward. The plastrals are paired, large, flat and nearly rectangular. They suggest by their appearance the plastron scutes. Their growth is inward and forward, as is that of their homologues in the plastron.

The two secondary dorsal rows, supramarginals and neuro-costals, consist anteriorly of small tubercles that fade out posteriorly into small irregular flat scales. The inframarginals are not tubercular but are rather large and fairly regular flat scutes. The interplastrals are diamond-shaped scutes forming a discontinuous row and occupying the angles made by four plastrals. This row is sometimes entirely absent on the tail-trunk of *Chelydra*.

It is clear then that in the tail and tail-trunk of *Chelydra* we have seven principal rows of scutes and between each pair of principal rows a secondary row, less regular and far less prominent. This would give a total of fourteen rows, of which seven are primary and seven secondary. Supposing that the carapace was originally continuous with the tail-trunk, we must imagine a gradual suppression of the secondary rows by the primary ones, until in the most highly specialized condition, seen in the terrestrial Emydidæ, only the seven primary rows have survived.

The order of loss of the seven secondary rows may be conjectured from an examination of the directions of encroachment of the principal rows upon the secondary rows. On this basis one might give the order of loss as follows: first, neuro-costals, which on account of inward encroachment of the costals and the outward encroachment of the neurals, would receive the severest pressure; second, the supramarginals located between the inwardly-encroaching marginals and the outwardly-encroaching costals; third, the interplastrals, between the two inwardly-encroaching plastrals, but occasionally able to escape pressure by occupying angles between four plastrals; fourth and last, the inframarginals, which were subject to pressure only on one side — that of the marginals — and were in addition required in more primitive forms with small plastrons to help bridge the space between the carapace and plastron. With the great increase in the size of the plastron which has taken place in higher forms, the space allotted to inframarginals became more and more contracted until they were crowded out entirely.

Does this order of loss correspond to any facts in nature? The same conclusion as to order of loss, I believe would be reached if we based our results on the prevalence, scarcity or absence of these rows as normal structures in existing species. No trace of neuro-costal scutes are found. Only one species, *Macrochelys temmincki*, possesses supramarginals. Interplastrals occur as isolated median ventral scutes in several families. Inframarginals occur normally in all the more primitive families and as axillaries and inguinals in all but the most specialized terrestrial forms.

This condition as derived from the tail-trunk of *Chelydra* differs rather radically from the ancestral condition derived from *Dermochelys*, in which there are twelve rows of equal rank. I am inclined to believe that *Dermochelys* is an extremely aberrant type with only a most distant connection with the phylogenetic line of *Chelonia*. The *twelve* keels of *Dermochelys* are comparable, I believe, to the *seven* keels of modern forms, and the irregular rows of plates and scutes between the keels are comparable to the secondary rows of scutes seen in the tail-trunk of *Chelydra* and represented in the carapace and plastron by inframarginals, supramarginals, interplastrals and neuro-caudals.

V. Further Evidence of the Former Existence of a Dermal Carapace in Chelonia, as Derived from Specimens of Graptemys.

The position just taken rests on the assumption that the carapace and plastron were at one time continuous with that portion of the trunk just posterior to them and that the carapace and plastron have undergone a gradual process of specialization that has caused them to depart widely from ancestral conditions. The tail-trunk would then preserve to a greater or less extent its original character.

On this assumption, then, there once existed a complete row of dermal tubercular ossicles overlying the vertebræ. That certain ancient forms did actually possess these ossicles was shown by Hay in the case of *Toxochelys serrifer*, but the question arises whether or not we have sufficient evidence that *Toxochelys* represents the ancestral condition of our modern forms.

For a long time I looked for definite traces, other than the keels, of such ossicles as are seen in *Toxochelys*, but met with no success until I had nearly completed the present paper. Then by merest chance I stumbled on the evidence needed to clinch the argument.

I had kept alive a few specimens of *Graptemys* in a small aquarium, but one by one they sickened and died, with one exception. Their death was doubtless due to the fact that this species is highly specialized in its diet, feeding exclusively on a species of viviparous gastropod that is abundant in Lake Maxinkuckee. They never learn to use other food, and, in lack of their special diet, starve themselves to death.

The surviving specimen was a nearly adult female that had been kept on account of its many peculiarities. After eleven months of captivity it was killed and examined for plate abnormalities. This examination revealed the presence of several small, loose, ossicles that were inlaid, as it were, in the bone of the neural plates and were situated beneath the keels of the second, third, fourth and fifth neural scales, *i. e.*, exactly in the positions occupied by the ossicles found in *Toxochelys*. The largest of these ossicles (see Fig. 5) was situated beneath the keel of the third scute and extended partially under the anterior margin of the fourth scute. The fifth scute is a supernumerary neural (No. 8) and hence the occurrence of an ossicle at its keel shows that it belongs in the neural row in spite of the fact that it is crowded to one side. All of the ossicles are imbedded or inlaid in the centers of certain of the neural plates. If they were merely the loosened centers of these plates, we would surely expect to find them on all the plates instead of just those which lie beneath the keels of the scutes. In what respect do these ossicles, then, differ from those seen in *Toxochelys serrifer* by Hay? Merely in this, that they are much reduced in size, so that each is confined to one neural plate, extending back so as to overlap the anterior portion of another plate.

The specimen is an oddity in many respects. It is unusually long in the carapace; possesses fifteen plates in the neural row instead of the normal number, twelve (three of these probably representing supernumerary procaudals); two extra costal plates or ribs, one quite vestigial; two supernumerary scutes of large size; one supernumerary costal scute of large size on the right side; and two well-developed supernumerary inframarginals on each side. Other minor peculiarities might be noted, but they do not concern the carapace or plastron. All of the anomalies mentioned may be viewed as of atavistic character, and it should not be surprising to find that the curious specimen shows an even more significant atavistic recurrence than any other specimen thus far examined, namely, a reversion to the condition seen in *Toxochelys*. That the genus *Graptemys* originally possessed a median dorsal keel composed of prominent bony tubercles covered with chitinous sheaths (scutes) is rendered extremely probable when we examine the young, especially that of *G. pseudogeographica*, a specimen of which is pictured in Agassiz' Contributions to the Natural History of the United States, Vol. II., Plate II., Figs. 11 and 12. This specimen, which may perhaps be an extreme type, although Agassiz does not suggest that such is the case, shows a series of three very remarkable dorsal tubercles on the second, third and fourth scutes. These tubercles furnish a close approximation in general form to those seen on the tail of *Chelydra*. It will be noted that these tubercles occur exactly in the places where I have found the vestigial ossicles in a specimen of *Graptemys geographica*, and that the most prominent tubercle is that on the third scute, a fact that is of interest in view of the larger size of the vestigial ossicle on that scute.

The adult of *Graptemys pseudogeographica* retains decided traces of these tubercles throughout life and their location is marked by dark blots of pigment that in later life form the only prominent color-markings of the animal. The discovery of vestigial ossicles in *Graptemys geographica* led me to investigate a very large female specimen of *Graptemys pseudogeographica*, that has been in confinement, and, like its relative, starving for many months. Immediately beneath the dark blots of pigment on the neural scutes there are on this specimen thin, scale-like discs of bone with a looser and less dense texture than the underlying bony plates. I have been able to examine but one adult specimen of *Graptemys pseudogeographica*, but this one appears to be perfectly normal in every other respect. It is to be noted that the vestigial plates in the last-mentioned specimen occupy exactly similar positions, with respect to scutes and plates, as do the vestigial ossicles in the anomalous specimen of *Graptemys geographica*, described and pictured above (Fig. 5). The probable explanation of both these conditions is that long-continued starvation has brought about a resorption of the portions that united these ossicles with the underlying neurals. That bone is resorbed either by normal processes or as the result of pathological conditions I have observed in several cases where holes have been eaten entirely through the bone of the carapace, as the result of starvation. Only a thin cap covering the top of the tubercle is of dermal origin, the main portion of the prominence being merely an outgrowth of the periosteum of the neural process. Examinations of developmental stages have revealed no discontinuity between the cap and the rest of the keel, but the microscope reveals the difference in histological structure between the cap and the underlying bony plate.

That tubercular ossicles existed over the neural processes of other ancient reptiles is shown by the fossil *Stegosaurus*. Here the dermal processes are very large and prominent and are much fewer in number than the neural processes that underlie them. This points to the entire independence of dermal bones and the vertebræ, and hence to the non-segmental character of the dermal plates.

VI. The Color Pattern of Chelonia as Confirmatory Evidence for the Former Existence of a Dermal Armor.

Evidence is not lacking that points to an original striped condition of the chelonian carapace. The neck and tail of most tortoises show characteristic stripes which on careful examination may be analyzed into rows of scales with similar coloration. When the scales are large enough, it will be seen that each has a center of pigmentation coinciding with its center of growth. Now the coloration of the carapace and plastron is nothing more than a series of scales or scutes, each with its pigmental center. The striped effect is lost through the great increase in the size of the scute and the consequent separation of the centers of pigmentation.

The pigmentation of scutes is typically concentric in character, whether the pattern consist, as in *Chelydra* and *Aromochelys*, of radiating bands of pigment having their center located at the center of scute growth, or concentric rings as in *Graptemys*, or lastly, of a light area occupying the center of growth, and all the rest solidly colored, as in *Clemmys guttatus*.

Frequently a great complexity of marking arises through the secondary complications of primary markings, but these conditions are seen in a simplified condition in the developmental stages.

It strikes one very forcibly that there is an intimate relation between scute growth and pigment distribution. The two processes have a common center and go hand in hand. The *areola*, or egg-plate (see Fig. 57, dotted lines) forms a convenient locus for measuring both processes. This location corresponds, curiously enough, with the keel of the scute and hence with the center of dermal ossification.

An examination of embryos of *Chelydra* shows that the coloration consists of dark patches of melanin pigment at the tip of the tubercular processes of the keels. The marginals are marked with small black spots at the posterior edge of each scute, sometimes running back over the anterior margin of the next scute. Specimens of *Chelydra* a year or two old have a radiating pattern with the center of pigment proliferation at the keel. In older specimens a solid coloration obscures everything.

Older embryos of *Graptemys* have, as the first indication of pigment, one dark spot at the median posterior margin of each scute, *i. e.*, at the keel (see Fig. 56). Later on two or more other spots of a similar appearance are produced in very definite positions on the various scutes. These secondary spots never become quite so prominent as the primary ones, but continue to develop like the latter into concentric ocellated markings (Fig. 57). The rings that constitute these ocellated spots are formed by repeated splitting of the innermost ring of pigment, in brief are proliferated from a center of pigment deposit. After three or four cencentric rings have been laid down, a well-marked unpigmented band appears on the periphery of the whole spot. It is this light band that produces the most pronounced secondary complexity, for it sends out processes to neighboring spots and forms the characteristic reticulated pattern that has given the name "map-turtle" to the species. In the marginals the pattern is not so complex, since no secondary spots appear. The concentric rings of the primary spot, however, often take on fantastic shapes that all but obscure the original unity of the coloration. It is very interesting to note that the spots in the marginal series are found as a rule half on one scute and half on the next, so that the light peripheral band that separates adjacent spots frequently coincides with the sutures of the dermal plates beneath. The spots then occupy the growth centers of the plates and no longer hold any close relationship with the scutes. *Pigmentation seems to be intimately connected with dermal ossification.* The scutes must have grown away from their original positions, thus overlapping the sutures of the plates, and lending strength to the general structure. The direction of movement has been forward, as is found by examination of the first pair of marginal scutes that run over upon the nuchal plate. The original cause of the forward movement was, I believe, the increase in size of the nuchal plate which must have pushed back the marginal plates. The scutes would of course occupy their original positions or would continue to crowd the nuchal scute into a still smaller space.

That the primary ocellated spots denote centers of dermal ossification will, I believe, be admitted. What then is the significance of secondary ocellated spots, which have an exactly similar appearance and method of development? They must, I believe, represent centers of dermal ossification and hence the location of scutes that formerly occupied the position now occupied by the spots. Evidences that serve to increase the probability of this conclusion may be adduced :

1. Whenever supernumerary scutes recur each has at its growth center an ocellated spot.

2. These supernumerary scutes come in at places where normal specimens have definitely placed secondary ocellated spots.

3. There are never any secondary ocellated markings on the marginal scutes, which agrees with our idea that the marginal rows contain nearly their original number of scutes and hence we would not expect to see traces of lost scutes in these rows.

4. The light bands that form the reticulated pattern of adult *Graptemys* have often the exact shapes of existing dermal plates. This is particularly the case in the procaudal region.

5. Considering the light bands as original scute boundaries, we can count ten costal scute areas in *Graptemys* or *Trachemys*.

6. On the neural scutes of *Graptemys* there are several much smaller ocellated spots that lie near the outer edges of the scute. These spots, I believe, are the vestiges of the small scutes that I have earlier designated as neuro-costals, and that were the earliest rows of scutes to be crowded out (Fig. 57). Four or more well-developed spots occur close to the marginals on the costals and occupy positions similar to the supramarginal scutes of *Macrochelys temmincki*.

At the angles made by adjacent neurals and costals occur ocellated spots that have the appearance of having been squeezed out between two scutes. These I believe to be the vestiges of the lost neurals and costals (see Fig. 57). When the lost scutes recur they have these spots at their growth centers.

In the bridge region of *Graptemys* and *Chrysemys* a confused series of dark colorations appears that seems to have no reference to any existing structures. But when the inframarginals recur, we find that these apparently meaningless markings fall into place as the spots of this lost row of scutes.

On the plastron scutes we find in most species a spot of pigment for each member, but confusing secondary complexity often obscures the real pattern. In *Graptemys* some specimens

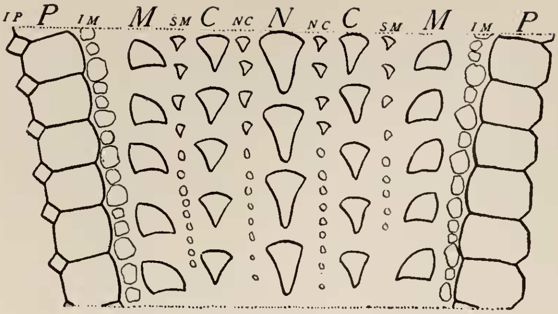

Fig. 55

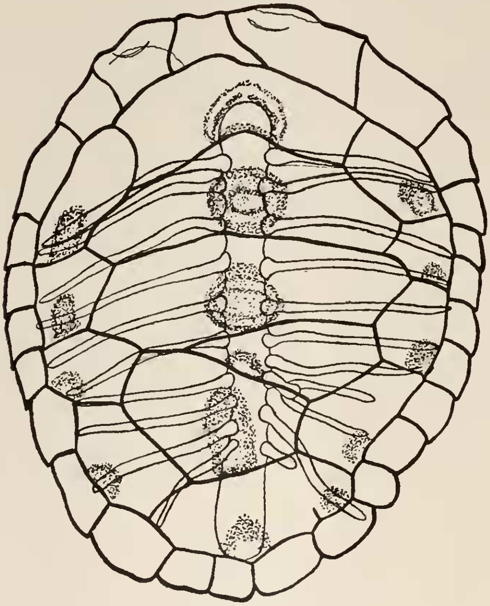

Fig. 56

Fig. 57

Fig. 58

show a fairly complete set of ocellated spots, but others show almost colorless scutes. Adult specimens seldom show any sign of pigmentation on the plastron. The markings then are largely juvenile in character and are subject to very great individual variation that tends toward the total obliteration of the original color pattern. An examination of a number of specimens, however, shows that each of the plastron scutes may have its ocellated spot.

The most confusing markings of all are those that occupy the median portion of the plastron in juvenile specimens. A remarkable secondary complexity of pattern has arisen in this region that would be almost impossible of solution were it not for the close series of stages leading up from the simplest conditions. The simplest form of marking consists of small diamond-shaped patches of pigment at the inner angles of the plastron scutes. These spread along the margins of the scutes, form bands by splitting, and finally produce the complex lyriform pattern that one finds quite frequently. The position of the simplest marking is identical with that of the hypothetical interplastral scutes and probably once constituted the color-marking of this row of scutes.

All of the carapace and plastron markings have thus been accounted for as the growth centers of existing or lost scutes. This has been done in a species with a highly intricate color pattern and could be applied successfully, I believe, to any other species.

It should be mentioned that the color pattern of *Graptemys* reaches its highest development in specimens of the first year. This is the time when protective coloration is a necessity, as the carapace is not sufficiently ossified to furnish a protection. Old specimens retain scarcely a trace of the original pattern, only a very faint reticulation being visible.

It might be suggested that the ocellated spots of the Trionychidæ are vestiges of scutes long since lost. The general number and arrangement of these spots tends to bear out this suggestion.

SUMMARY.

Palæontological and embryological evidence is at variance as to the origin and character of the neural and costal plates, but observations point strongly to a periosteal origin of these structures, which means that they are in no sense dermal or the descendants of the original dermal carapace.

The testimony of comparative anatomy leads to the belief that the nuchal, procaudal, pygal and marginal plates are the remnants of a once more or less complete dermal carapace and that these plates formed the cores of scutes that must have had a more or less tubercular form. The keels of existing scutes represent these tubercules. The testimony of the tail-trunk of *Chelydra* indicates that there were originally seven primary rows of such scutes and that less prominent rows of scutes occupied the interspaces. These less prominent rows were gradually suppressed, first on the carapace and then on the plastron, beginning in the middle and proceeding laterally. Thus the first loss was the neuro-costal rows, second the supra-marginals, third the interplastrals, and fourth the inframarginals, which to-day persists normally in many primitive forms.

Accompanying the suppression of rows occurred a reduction in the number of scutes in the primary rows, and this reduction took a general antero-posterior direction. At the same time the rapid secondary growth of the neural spines and ribs caused the suppression of the corresponding dermal plates, leaving only the nuchal, procaudals, pygal and marginals in places where the internal skeletal portions failed to extend. Traces of the dermal armor in the mid-neural region have been found, however, in *Toxochelys* and *Graptemys.*

No correlation of abnormalities is to be expected in the neural and costal regions, since the scutes and plates of this region are entirely independent in origin, but in the marginal series, where the plates and scutes retain nearly their original connections, the correlation is perfect. In the procaudal region we find frequent correlations, but, that the correlation is not a necessary one, is shown by numerous uncorrelated abnormalities.

A study of the color-markings of *Graptemys* and *Chelydra* lends confirmation to all the above theories of the chelonian carapace and plastron, and at the same time serves to rationalize the patterns themselves.

BIBLIOGRAPHY.

Agassiz, L.
'57 Contributions to the Natural History of the United States, Vol. II., 1857.

Baur, G.
'96 Bemerkungen uber die Phylogenie der Schildkröten. Anat. Anz., Bd. 12, No. 24/25, 1896.

Baur, G.
'89 On the Morphogeny of the Carapace of the Testudinata. Amer. Nat., XXI., 1889.

Baur, G.
Die systematische Stellung von Dermochelys. Biol. Centralbl., Bd. IX.

Bemmelen, J. F. van
'96 Bemerkunger über den Schadelbau von Dermochelys coriacea. Gegenbauer Festschrift II., 1896.

Bienz, A.
'95 Dermatemys mavii, Grey. Eine osteologische Studie mit Beiträgen zur Kentniss vom Bau der Schildkröten. Rev. Suisse Zool., III., 1895.

Coker, R. E.
'05 Gadow's Hypothesis of "Orthogenetic Variation in Chelonia." Johns Hopkins Univ. circular, No. 178, May, 1905.

Cope, Edw. D.
'96 The Ancestry of the Testudinata. Amer. Nat., Vol. 30, 1896.

Dollo, M. L.
'86 Première Note sur le Cheloniens du Bruxellien (Èocène Moyen) de la Belgique. Pamphlet. 1886.

Gadow, H.
'99 Orthogenetic Variation in the Shells of Chelonia. Zool. Results. Willey, A., 1899.

Gadow, H.
'01 Amphibia and Reptiles. The Cambridge Nat. Hist., Vol. VIII., 1901.

Gegenbauer, C.
Vergleichende Anatomie der Wirbeltheire. Erster Band, Leipzig, 1898.

Goette, A.
'99 Uber die Entwicklung des knockeren Rückenschilds der Schildkröten. Zeit. f. wiss. Zool., Bd. LXVI., 1899.

Gray, J. E.
'55 Catalogue of Shield Reptiles in the Collection of the British Museum. Part I. London, 1855.

Harrison, R. G.
The Growth and Regeneration of the Tail of the Frog Larva. Arch. f. Entwicklungsmechanic d. Organism. Bd. VII., pp. 431–485.

Hay, O. P.
'91 The Batrachians and Reptiles of Indiana. 17th Report of the State Geologist, 1891.

Hay, O. P.
'97 On Protostega, the systematic position of Dermochelys, and the Morphogeny of the Chelonian Carapace and Plastron. Amer. Nat., XXXII., 1897.

Hay, O. P.
'00 The Composition of the Shell of Turtles. Science, Vol. 13, p. 624. 1900.

Haycraft, J. B.

'90 The Development of the Carapace of Chelonia. Trans. R. Soc Edinb., XXXVI, 1890.

Jordan, D S

'99 A Manual of the Vertebrate Animals of the Northern U. S. 1899.

Owen, R.

'49 On the Development and Homologies of the Carapace and Plastron of Chelonian Reptiles. Phil. Trans., Lond., 1849.

Parker, G. H.

'01 Correlated Abnormalities in the Scutes and Bony Plates of the Sculptured Tortoise. Amer. Nat., Vol. 35, 1901.

Rathke, H.

'48 Ueber die Entwicklung der Schildkröten. 1848.

Schoepff, J D.

'92 Historia Testudinum. 1792.

Stoffert, A. T.

'89 Bau und Entwicklung der Schaale von Emyda ceylonensis. Basel, 1889.

Van Lidth de Jeude, Th. W.

'98 On Abnormal Pectoral Shields in Testudo ephippium. Notes Leyden Mus., Vol. 20, 1898.

Wandolleck, B.

'04 An Abnormal Tortoise. Zool. Jahrb., XX., pp. 151–166, 1904.

Werner, F.

'95 Bemerkunger uber Schildkröten-zeichnung. Biol. Centralbl., Bd. 14, 1895.